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Mapping Quantitative Trait Loci for Carcass and Meat Quality Traits in a Wild Boar × Large White Intercross[1]

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ABSTRACT: An intercross between wild boar and a domestic Large White pig population was used to map quantitative trait loci (QTL) for body proportions, weight of internal organs, carcass composition, and meat quality. The results concerning growth traits and fat deposition traits have been reported elsewhere. In the present study, all 200 F_2 animals, their parents, and their grandparents were genotyped for 236 markers. The marker genotypes were used to calculate the additive and dominance coefficients at fixed positions in the genome of each F_2 animal, and the trait values were regressed onto these coefficients in intervals of 1 cM. In addition, the effect of proportion of wild boar alleles was tested for each chromosome. Significant QTL effects were found for percentage lean meat and percentage lean meat plus bone in various cuts, proportion of bone in relation to lean meat in ham, muscle area, and carcass length. The significant QTL were located on chromosomes 2, 3, 4, and 8. Each QTL explained 9 to 16% of the residual variance of the traits. Gene action for most QTL was largely additive. For meat quality traits, there were no QTL that reached the significance threshold. However, the average proportion of wild boar alleles across the genome had highly significant effects on reflectance and drip loss. The results show that there are several chromosome regions with a considerable effect on carcass traits in pigs.

Key Words: Gene Mapping, Quantitative Traits, Carcass Composition, Meat Quality, Wild Pigs

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Introduction

There are several advantages in using crosses between divergent populations in studies designed to map quantitative trait loci (**QTL**) in domestic animals. Alleles with large effects segregate in the intercross, a relatively high marker heterozygosity improves the information content compared to-within population studies, and high heterozygosity at the QTL in addition to consistent linkage phases make the statistical analyses powerful (Andersson et al., 1997). A disadvantage from a practical breeding perspective is that the QTL detected may not be segregating within the commercial populations of interest. However, a population with overall inferior performance can contain genes that enhance performance or product quality (Xlao et al., 1996). Thus, some of the detected QTL may be of great interest for introgression into commercial populations.

In the present study, we used an intercross between wild boar and a domestic Large White population. Due to the process of domestication and controlled selection, these populations show marked phenotypic differences for many traits. Therefore, data for a large number of traits were collected on live animals and carcasses from the F_2 generation. The results concerning growth and fat deposition traits have been reported elsewhere (Andersson et al., 1994). The objective of the present study was to map QTL for body proportions, weight of internal organs, carcass composition, and meat quality.

Materials and Methods

Animals. Two European wild boars were mated to eight Large White (Swedish Yorkshire) sows. Four sires and 22 dams of their offspring, the F_1 generation,

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were parents of 200 F_2 animals. To get large full-sib families, most sows were mated to the same boar for the first and second litters. The F_2 animals were reared in two batches with two feeding treatments in each at the pig experiment station of the Swedish University of Agricultural Sciences in Uppsala (Lundström et al., 1995). Male pigs of the F_2 generation were castrated.

Marker Map. The study was based on marker information from a comprehensive linkage map, including 236 markers with a total map length of about 2,300 cM (i.e., an average marker distance of 10 cM). Markers were available on all of the 18 autosomes, with between five and 20 markers on each (Marklund et al., 1996). The animals of all three generations were genotyped.

Phenotypic Data. The F_2 animals were slaughtered at a live weight of at least 80 kg or at a maximum age of 190 d, and the weights of internal organs were recorded. Two days after slaughter, the chilled carcasses were parted and divided into ham, back, belly, and shoulder. The ham and back were defatted and fully dissected. Meat quality traits (i.e., meat color, water-holding capacity, ultimate pH, protein extractability, and shear force) were determined for the longissimus muscle unless otherwise stated. Carcass assessment methods and meat quality measurements are further described in Lundström et al. (1995). The analyzed traits are specified in Table 1.

Statistical Analyses. Following Haley et al. (1994), the marker genotypes were used to estimate the probabilities of the breed origin of each gamete at fixed 1-cM intervals through the genome for each F_2 animal. These probabilities were used to calculate additive and dominance coefficients for a putative QTL at each position under the assumption that the QTL was fixed for alternative alleles in the two breeds. The trait values were then regressed onto these coefficients in intervals of 1 cM. A test for the presence of an additional linked QTL was performed on each chromosome with a significant QTL effect by comparison of the best model with two QTL in any positions in the linkage group with the best model with a single QTL (Haley and Knott, 1992). The threshold values for the genome-wide significance level were set by simulation studies as described in Andersson et al. (1994). The *F*-ratios corresponding to the 10, 5, and 1% significance levels were 7.8, 8.6, and 10.4, respectively.

The marker genotypes were also used to calculate the probability that each F_2 animal had inherited the wild boar alleles at fixed positions in the genome. These probabilities were then averaged over each autosome and over all 18 autosomes. The effect of proportion of wild boar alleles was tested as a regression for each chromosome and for the whole genome, respectively. In the chromosome-wise analysis a standard Bonferroni correction for the 18 independent tests was made to get an overall significance level (P) comparable to the genome-wide threshold used in the separate analyses of all map positions: $P = 1 - (1 - \alpha)^{18}$.

Table 1. Analyzed traits with phenotypic means, standard deviations, and number of F_2 animals with data

Trait	Mean	SD	No.
Body proportions			
Carcass wt, kg[a]	61.0	7.1	191
Dissected carcass half wt, kg[b]	28.2	3.2	191
Carcass length, cm[c]	90.1	3.6	190
Distance vertebrae, cm[d]	65.4	2.6	190
Head width, cm	14.4	.6	103
Weight of internal organs			
Heart wt, g	234	28.8	188
Liver wt, g	1402	181.6	188
Kidney wt, g	244	35.3	182
Spleen wt, g	124	22.5	183
Carcass composition			
Lean meat in ham, %	64.8	3.6	191
Bone/lean meat in ham, %	5.8	.6	191
Lean meat + bone in ham + back, %	73.4	4.2	191
Lean meat + bone in back, %	67.4	5.4	191
Longissimus muscle in back, %	32.4	4.0	190
Longissimus muscle area, cm^2	33.4	4.2	187
Meat quality			
pH_u, longissimus muscle	5.6	.3	173
pH_u, biceps muscle	5.9	.3	173
Drip loss, %	5.1	1.9	190
Filter paper wetness, (0–4)	2.0	1.2	191
Reflectance value, EEL	18.7	4.5	190
Pigmentation, ppm hematin	38.3	6.6	190
Total protein extractability, mg/g	140.6	44.6	190
Sarcoplasmic protein extractability, mg/g	68.0	11.3	190
Shear force, kg/cm^2	4.9	.9	189

[a]Carcass with head.
[b]The sum of the weights of cuts of the dissected carcass half.
[c]Measured between the bottom of the atlas vertebra and the anterior edge of the pubic bone.
[d]Measured as distance between first thoracic and last lumbar vertebra.

In addition to the regressions on the additive and dominance coefficients or the proportion of wild boar alleles, statistical models included the fixed effects and covariates that were relevant and significant for the respective trait (Table 2). Carcass weight among the F_2 animals ranged from 43 to 79 kg (Table 1). To discern QTL effects on correlated traits, carcass weight was included as a covariate. Therefore, all results concerning body length and carcass composition were compared at equal carcass weights. To account for background genetic effects, family and significant unlinked QTL were included in the analyses.

The halothane mutation at the CRC locus, Hal^n (Fujii et al., 1991), was present in the heterozygous form in one of the two founder wild boars but not in any of the founder sows. Lundström et al. (1995) showed that Hal^n had a significant effect on meat content and meat quality in the present material. This was reported to be an effect of the particular allele and

Table 2. Fixed effects and covariates included in the statistical models in analyses of different types of traits

	Fixed effects				Covariates	
Trait	Sex	Family	Feeding[a]	CRC[b]	Carcass wt	Age at slaughter
Body proportions						
Carcass wt traits		X	X			
Carcass length traits		X	X		X	
Head width		X	X		X	
Weight of internal organs						
All traits	X	X	X		X	
Carcass composition						
All traits	X	X	X	X	X	
Meat quality						
pH in muscles		X	X	X		
Water-holding capacity		X	X	X		X
Meat color		X	X	X		X
Protein extractability		X	X	X		
Shear force		X	X	X		X

[a]Feeding regimen within parity number.
[b]Presence/absence of the halothane mutation (Hal^n) at the *CRC* locus; see text.

not of a difference between alleles originating from the wild boars and the domestic sows. Therefore, in analyses of carcass composition and meat quality traits, genotypes at the *CRC* locus were included in the model. Genotypes were divided in two classes corresponding to Hal^N/Hal^N and Hal^N/Hal^n.

Residuals of all traits were tested for normality according to the Shapiro-Wilk test (SAS, 1989). Only a few traits deviated significantly from a normal distribution. For three morphological traits, the deviation was fully explained by one or two outliers each, which were removed from the data. The distributions of the uncorrected pH-values were clearly bimodal, such that a small group of 18 animals had a value of 5.97 or higher as ultimate pH in the longissimus muscle. The animals belonged to 16 families, and a preliminary LOD score analysis, assuming that these extreme animals were homozygous for a recessive allele, did not indicate that the bimodal distribution had a simple genetic background. The abnormal pH-values were most likely due to environmental stress causing a lack of glycogen in the muscles of some animals. We excluded the group of animals with the abnormal pH-values when analyzing the pH traits. The remaining datasets were considerably closer to the normal distribution after fitting the model, even if they still deviated significantly ($P \approx .02$ as compared to $P \approx .0001$ when including the 18 outliers). Pigmentation, measured as the concentration of hematin in the longissimus muscle, had a positively skewed distribution after fitting the model. The skewness could not be explained by a few outliers. A second dataset was prepared for this trait by performing a logarithmic transformation, after which normally distributed residuals were obtained.

Results

Body Proportions. We found a QTL at the proximal part of chromosome 8 with an effect ($P < .01$) on body length (Figure 1a). The additive effect of the wild boar allele was estimated to be −1.2 cm in carcass length at equal carcass weight (Table 3). The proportion of wild boar alleles over the genome showed a significant effect on body weight such that an increased proportion of wild boar alleles reduced body weight. This effect was largely due to effects of chromosome 4, 7, and 8 acting in the same direction (Table 4). However, there were no single QTL with significant effects on body weight. An increase in the proportion of wild boar alleles on chromosome 15 significantly reduced the width of the head (Table 4).

Weight of Internal Organs. The only significant effect was a decrease in liver weight at equal carcass weight with an increased proportion of wild boar alleles. This significant genome effect was mainly caused by effects of three concurrent (nonsignificant) chromosome effects (Table 4).

Carcass Composition. We located a QTL with an impact ($P < .05$) on proportion of lean meat plus bone as well as lean meat content ($P < .10$) at the proximal end of chromosome 2 (Figure 1b). The additive effect of the wild boar allele at this QTL was between −1.3 and −2.0% of the weight of the respective cut.

We found strong evidence ($P < .01$) for a QTL on chromosome 4 affecting the proportion of lean meat plus bone, which is the complementary trait to fat percentage, in different cuts of the carcass (Figure 1c; Table 3). The additive effect of the wild boar allele was negative (−1.7 to −2.4% of the cuts), and there was also an indication of a dominance effect at this QTL. A QTL influencing ($P < .05$) the proportion of bone in relation to lean meat in ham was located more

Table 3. Test statistics (highest F-ratios), map positions, estimates of quantitative trait loci (QTL) effects, and percentage of the residual variance explained by QTL for body proportions and carcass composition

Trait	*F*-ratio[a]	Map position[b]		Additive[c] effect	Dominance[d] effect	MSE_{red}[e]
		Chr	cM			
Body proportions						
Carcass length, cm	11.2**	8	9	−1.20 ± .25	−.11 ± .34	11.3
Distance vertebrae, cm	10.7**	8	5	−1.07 ± .24	−.39 ± .34	10.8
Carcass composition						
Lean meat in ham, %	7.9†	2	10	−1.32 ± .33	−.20 ± .53	8.0
Bone/lean meat in ham, %	9.8*	4	88	−.22 ± .05	.04 ± .07	10.0
	9.1*	8	10	−.20 ± .05	.16 ± .07	9.3
Lean meat + bone in ham + back, %	9.4*	2	8	−1.62 ± .37	−.01 ± .58	9.7
	12.7**	4	49	−1.69 ± .36	−.88 ± .52	13.0
Lean meat + bone in back, %	9.2*	2	7	−1.99 ± .46	−.05 ± .71	9.4
	16.5**	4	49	−2.42 ± .45	−1.37 ± .66	16.4
Longissimus muscle area, cm^2	8.7*	3	79	1.55 ± .37	−.20 ± .50	9.0

[a]Genome-wide significance levels: †$P < .10$; *$P < .05$; **$P < .01$.
[b]Map position is the one giving the highest test statistic (*F*-ratio) on that chromosome estimated in centimorgans from the proximal end as defined in Marklund et al. (1996). Chr = chromosome.
[c]Additive effect of a QTL defined as the deviation of animals homozygous for the wild boar allele from the mean of the two homozygotes; estimate given with standard error.
[d]Dominance effect of a QTL defined as the deviation of animals heterozygous for the wild boar allele from the mean of the two homozygotes; estimate given with standard error.
[e]MSE_{red} = Reduction in residual variance of the F_2 population due to the inclusion of a QTL at the given map position.

Table 4. Test statistics for the effect of proportion wild boar alleles averaged over the whole genome and over each autosome, respectively (only chromosome effects with nominal $P < .05$ are shown)

Trait	Genome average[a]		Chromosome averages[b]
	F-ratio	Estimated effect	
Body proportions			
Carcass wt, kg	24.2***	−40.5 ± 8.2	C4† (−); C7* (−); C8* (−)
Dissected carcass half wt, kg	22.5***	−18.4 ± 3.9	C4 (−); C7* (−); C8† (−)
Carcass length, cm	1.6		C4 (−); C8* (−)
Distance vertebrae, cm	2.2		C4 (−); C6 (−); C8† (−)
Head width, cm	3.2†	−1.7 ± .9	C15* (−)
Weight of internal organs			
Heart wt, g	.6		C3 (+); C6 (−); C13 (+)
Liver wt, g	5.8*	−513 ± 213	C4 (−); C6 (−); C14 (−)
Kidney wt, g	1.9		C5† (−)
Spleen wt, g	.6		C3 (+); C5 (−); C7 (+)
Carcass composition			
Lean meat in ham, %	.4		C2 (−)
Bone/lean meat in ham, %	5.7*	−1.8 ± .8	C4* (−); C7 (−); C8* (−)
Lean meat + bone in ham + back, %	5.5*	−12.8 ± 5.5	C2 (−); C4** (−)
Lean meat + bone in back, %	9.0**	−21.0 ± 7.0	C2 (−); C4** (−)
Longissimus muscle in back, %	.5		
Longissimus muscle area, cm^2	.3		C3 (+); C8* (+)
Meat quality			
pH_u, longissimus muscle	.0		C4 (−)
pH_u, biceps muscle	.9		
Drip loss, %	7.8**	−7.9 ± 2.8	C1† (−); C2 (−); C12† (−)
Filter paper wetness, (0–4)	1.9		C12 (−); C13 (−); C18 (−)
Reflectance value, EEL	8.2**	−17.4 ± 6.1	C2 (−); C10 (−); C12 (−); C15 (−)
Pigmentation, ln (ppm hematin)	.5		C2 (−); C15† (+)
Total protein extractability, mg/g	.0		
Sarcoplasmic protein extractability, mg/g	1.5		C2 (+)
Shear force, kg/cm^2	.0		C3 (−)

[a]*F*-value, genome-wide significance level, and estimated regression of the respective trait on the wild boar proportion (genome average). Genome-wide significance levels: †$P < .10$; *$P < .05$; **$P < .01$; ***$P < .001$.
[b]Chromosome number, genome-wide significance level, and direction of the regression of the respective trait on the wild boar proportions (chromosome averages). Genome-wide significance levels: †$P < .10$; *$P < .05$; **$P < .01$.

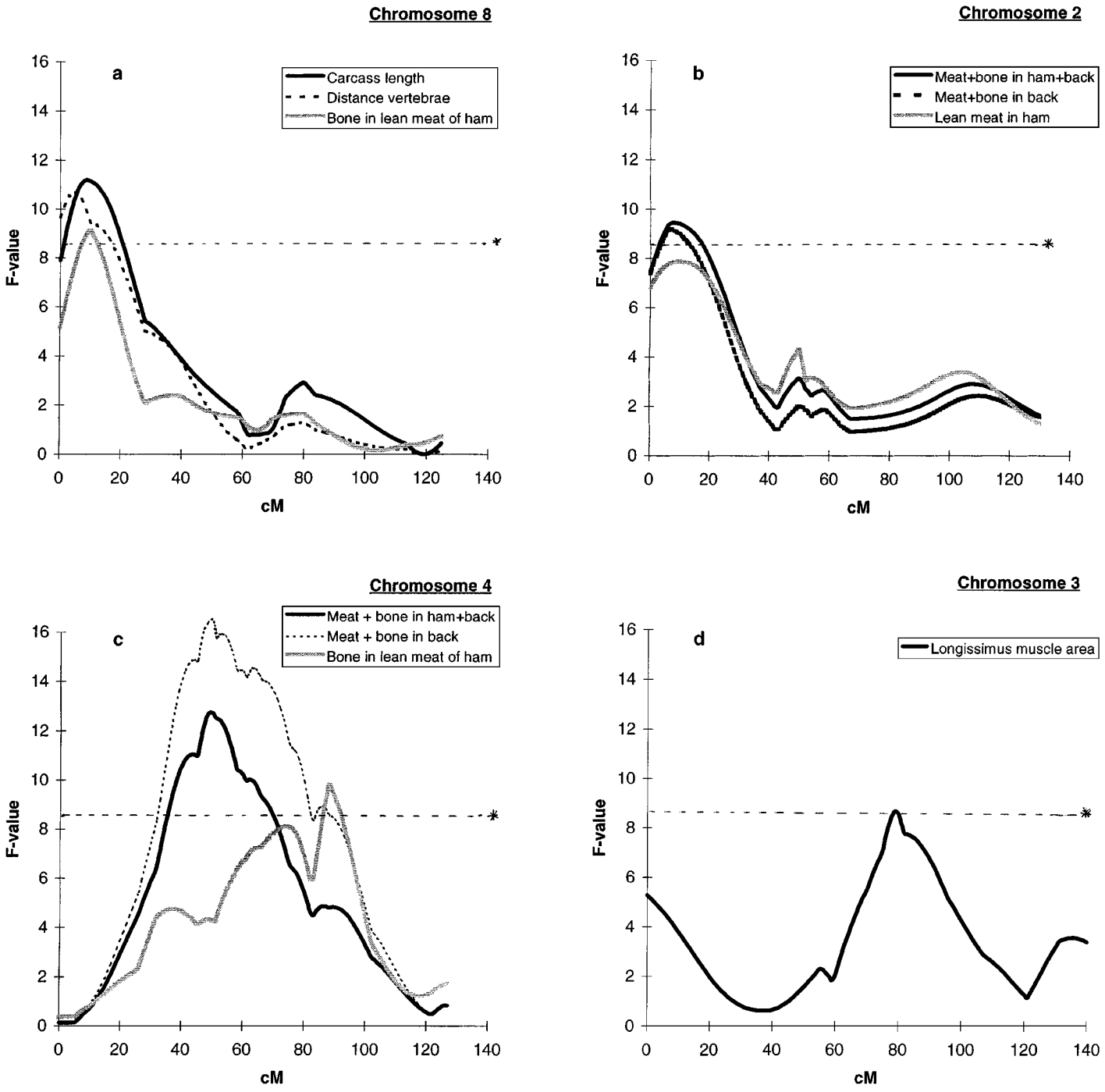

Figure 1. Test statistic curves for chromosomes 8 (a), 2 (b), 4 (c), and 3 (d). Horizontal dotted lines indicate the 5% genome-wide significance thresholds.

distally on chromosome 4. The same trait was also influenced ($P < .05$) by a QTL at the proximal part of chromosome 8 (Figure 1a; Table 3).

A QTL with a positive additive effect of the wild boar allele on longissimus muscle area was located on chromosome 3. The error variance was reduced by 9% by including the QTL in the model (Figure 1d; Table 3). By adding the effect of a second QTL at the proximal end of chromosome 3, the error variance was reduced by another 7%. The *F*-ratio for the test of two vs one QTL on chromosome 3 was 6.8. The two QTL had counteracting effects, and the average proportion of wild boar alleles of the chromosome was not significant. The proportion of wild boar alleles of chromosome 8 showed a significant positive correlation to the longissimus muscle area (Table 4).

Meat Quality. At chromosome 2 there were indications of effects on meat quality traits (i.e., meat color and water-holding capacity), but these effects did not reach statistical significance (*F*-ratios 4.8 to 6.3). The

average proportion of wild boar alleles across the genome had significant effects on reflectance and drip loss; increased proportion yielded darker meat with lower drip loss. The significant genome effects were caused by effects of several chromosomes, all having the same direction (Table 4).

Discussion

In the present study, we found significant QTL effects for carcass composition and(or) body proportion traits on chromosomes 2, 3, 4, and 8. All effects but one had the direction that could be expected, the wild boar alleles giving a shorter and less meaty carcass at equal carcass weight. However, the wild boar allele of one of the QTL on chromosome 3 increased the longissimus muscle area by 1.5 cm^2. This QTL could be of some interest from a practical breeding point of view.

Each detected QTL accounted for at least 9% of the residual variance in the F_2 generation. The minimum size of effects that are detected depends on the applied significance thresholds, the information content of the marker map, and the design and size of the experiment. Van Ooijen (1992) investigated the accuracy of QTL mapping by simulations in first-generation backcross and F_2 populations of different sizes; for example, an F_2 population of size 200, which is comparable to that in the present study. He found that 79% of the QTL explaining 10% of the total variance were detected, whereas only 29% of the QTL explaining 5% of the variance obtained a significant test statistic. Thus, the probability of detecting QTL with small effects was very limited in the present study.

The QTL with the largest effect explained more than 16% of the residual variance in proportion of lean meat plus bone in the back. This QTL, located on chromosome 4, is most likely identical to the previously reported QTL for abdominal fat and backfat depth (Andersson et al., 1994), which has been confirmed in subsequent generations (Marklund et al., unpublished data). This was the only QTL found at which there was an indication of dominance effects. The result agrees well with Andersson et al. (1994), who reported that there was an indication of dominance for increased backfat depth on chromosome 4. For all other QTL, gene action seemed to be largely additive. The QTL influencing proportion of bone in relation to lean meat in ham, located at the distal end of chromosome 4, could be the same as the one reported to have an effect on growth rate in Andersson et al. (1994).

We did not find any significant interaction between the QTL and fixed effects of sex or CRC class. The existence of such interactions still cannot be excluded because the power of the tests for interaction was relatively low due to the limited size of the experiment. The limited number of animals also made testing of epistatic effects unfeasible in the present study. There was no evidence of more than one QTL on the same chromosome for any of the traits, except for longissimus muscle area. The proportion of the residual variance explained by an additional QTL was for all other traits below 3%. However, there were some traits for which there were no significant QTL detected, but one or more chromosomes with significant effect of the average proportion wild boar alleles. The test-statistic curves of those chromosomes often had two or more peaks and(or) a flat profile (data not shown). A possible explanation for these effects of average proportion of wild boar alleles, across chromosomes or across the whole genome, could be segregating oligo- and(or) polygenes with an impact on the traits.

Animals in the F_2 generation had an average proportion of wild boar alleles of 50%, as expected. The range was 35 to 66%. The regression of the traits on the average proportion wild boar alleles can therefore give us an estimate of the effect of using wild boar crosses in commercial crossbreeding systems. For every 10% increase in wild boar proportion we can, at average carcass weight, expect proportion fat in the valuable cuts ham and back to increase 1 to 2 percentage units, proportion bone to lean meat in ham to decrease .2 percentage units, reflectance value to decrease 2 EEL-units, and drip loss to decrease .8 percentage units. Very little data have, to our knowledge, been published comparing wild boars or wild boar crosses to domestic pigs under equal circumstances. Concerning carcass traits, Clausen and Gerwig (1955) found that carcass length decreased and fat content increased with an increasing proportion wild pig in crosses with Danish Landrace. In the present study, we did not find any significant overall effect of wild boar proportion on carcass length, even though the wild boar allele of a QTL on chromosome 8 significantly decreased carcass length. Neither did we find the effect on shear force values that was reported in two previous studies (Townsend et al., 1978; Rede et al., 1986). However, conclusions concerning the presence and size of breed differences must be treated cautiously because all information concerning the wild boar breed in the present study originates from only two founder animals.

The total number of traits analyzed in the present study was 24. Many of them were highly correlated. A principal component analysis (SAS, 1989) showed that 11 independent components explained more than 90% of the total variation. If a Bonferroni correction for 11 independent tests is made, only one of the detected QTL (F-ratio > 12.0) is significant with an overall type I error below 5%. However, this is a very conservative test, and there is currently scientific discussion on how to set threshold values and how to interpret results from QTL mapping studies. Lander and Kruglyak (1995) proposed the reporting of suggestive linkages and significant linkages, using the

probability of 5% as threshold for significant linkage in a genome scan. They pointed out that significant linkages will turn out to be false positives once in 20 genome scans. In the present study, we found evidence for at least four QTL in a total of 24 genome scans (or 11 independent scans) using the 5% threshold. Our conclusion is therefore that we have found true QTL influencing carcass composition and body proportions. Yet, we agree with Lander and Kruglyak (1995), who stressed that significant linkages must be confirmed by replication to be credible.

We have chosen to give the results of all analyses in an appendix that can be requested from the authors. In the appendix, the highest test statistics and best positions are given for all chromosomes and all traits. The size of most experiments with large farm animals is relatively low due to the experimental costs, and the statistical power of the analyses is therefore limited. In setting stringent significant thresholds we expect a high rate of type II errors; we fail to detect many real QTL, each explaining a small proportion of the total variation. In the near future, results from several QTL mapping experiments will be presented. If all results from the experiments were made available it would be possible to perform global meta-analyses summarizing data across experiments, thus increasing the possibilities of locating QTL with small effects. We suggest that Web sites are good fora for such information, and that a debate on the appropriate amount and format of the information to be stored is needed.

Implications

The findings of the present study give us an increased knowledge of the inheritance of carcass and meat quality traits in pigs. In all identified chromosome regions but one, the wild boar alleles gave a shorter and less meaty carcass. However, in one region the wild boar allele increased longissimus muscle area. The results indicate that wild boars may carry some favorable quantitative trait loci alleles that may be exploited by introgression and marker-assisted selection. The study also gives estimates of the effects on carcass traits when using wild boar in crossbreeding systems.

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